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16. ABSTRACT

Studies concerning the impact of UV-B radiation upon terrestrial organisms have been conducted in the laboratory, in growth chambers and greenhouses, and a few under fairly natural "field" conditions. Detrimental effects were noted for growth, morphology, and function in a large variety of plants species, including many important agronomic crops such as soybeans. Of note is the fact that elimination of the UV-B waveband from natural solar radiation usually benefits the organism or system under investigation. This fact indicates that even current levels of UV-B radiation have a negative impact upon some life processes. Whether enhanced levels would have a relatively greater impact requires further field validation of laboratory studies. In aquatic systems there is good evidence that current levels of solar ultraviolet radiation depress near-surface primary productivity. Marine animals may tolerate current levels of solar UV-B radiation by means of protective screens, avoidance behavior, and repair processes which reverse much of the potential damage inflicted by the radiation. For all of the aquatic studies conducted in the laboratory great caution must be exercised when relating the results to a natural body of water. To be considered are such factors as the depth of the attenuating water column, mixing, the ratio of photosynthetically active radiation to UV-B radiation, behavioral responses, seasonality of exposure, and the prehistory of the target organisms...

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IMPACT OF UV-B RADIATION UPON NONHUMAN ORGANISMS

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For years, scientists and laymen alike have casually noted the impact of solar ultraviolet radiation upon the nonhuman component of the biosphere. It was not until recently, when human activities were thought to threaten the protective stratospheric ozone shield, that researchers undertook intensive studies into the biological stress caused by the previously slightly short-wavelength edge of the global solar spectrum. It is stratospheric ozone that functions effectively as an ultraviolet screen, filtering out solar radiation in the 220-320 nm waveband as it penetrates through the atmosphere, allowing only small amounts of the longer wavelengths of radiation in this waveband to leak through to the surface of the earth. Although this radiation (UV-B radiation, 290-320 nm) comprises only a minute fraction (less than 2%) of the total solar spectrum, it can have a major impact on biological systems due to its actinic nature. Many organic molecules, most notably DNA, absorb UV-B radiation which can initiate photochemical reactions. It is Life's ability, or lack thereof, to cope with enhanced levels of solar UV-B radiation that has generated the concern over the potential depletion of stratospheric ozone. The defense mechanisms that serve to protect both plants and animals from current levels of UV-B radiation are quite varied. Whether these mechanisms will suffice under conditions of enhanced levels of UV-B radiation is the subject of this paper.

Agricultural Crops, Native Terrestrial Vegetation, and Marine Phytoplankton

Although some forms of plant life are motile and exhibit negative phototaxis in response to ultraviolet (UV) radiation, the avoidance of UV radiation for most plants does not include escape movements [1]. Unlike animals, which can reduce exposure of their

tissues to solar radiation through protective coverings and behavioral responses, terrestrial plants have evolved to expose much of their tissue to sunlight to utilize its energy for photosynthesis.

Many studies have demonstrated that photosynthesis is inhibited by UV-B radiation [2-9]. In addition, UV-B radiation can affect leaf expansion and abscisic acid content [3, 4, 10-16], pigment concentrations [12, 17-20], plant growth [8, 10, 17, 21-23], carbohydrate metabolism [24], fruit growth and yield [15, 25], and pollen germination and pollen tube growth [26].

In marine systems, UV-B radiation (e.g., 310 nm) penetrates approximately the upper 10% of the coastal marine euphotic zone before it is reduced to 1% of its surface irradiance [27]. There is good evidence that current levels of UV radiation depress near-surface primary production in marine waters. Steemann Nielsen [28] noted that the UV component of sunlight was capable of depressing both the rate of light-saturated photosynthesis and the initial slope of the Photosynthesis-versus-Irradiance curves for water samples from Frida Harbor, Washington. Jitts et al. [29] also found that surface samples from marine waters underwent greater primary production when covered with a UV-B filter than when exposed to full sunlight. The authors speculated that most reports for primary production in surface waters are overestimated by about 40% due to the common use of thick-walled glass bottles in the studies. Several other authors have also described the impact of UV-B radiation upon marine primary production [30-36]. Furthermore UV-B radiation impacts survival [37 and growth rate [33, 38].

Terrestrial and Marine Animals

Very little informatin has been published regarding the impact of UV-B radiation on nonhuman, terrestrial animals. Solar UV-B radiation is the probable cause of ocular squamous cell carcinoma (cancer eye) [39-41]. Cancer eye is found in most breeds of cattle, but it is most preyalent in the Hereford breed. Certain strains of the Hereford breed lack any pigment around the eye. UV-B radiation also acts as a significant enhancing factor in the etiology of keratitis in cattle [42] and reindeer [43]. The two-spotted spider mite can discriminate and respond to the presence of UV-B radiation [44]. In the study, the egg-laying capacity of the female mite was reduced in a linear fashion as the UV-B dose was increased. Radiation in the 320-400 nm waveband did not elicit either result.

Information exists regarding the impact of UV radiation on finfish raised in hatcheries [45, 46]; however, until recently, little documentation has appeared in the literature concerning UV stress upon pelagic fishes. Marinaro and Bernard [47] concluded from their study that solar UV radiation may be a stressful agent for pelagic fish eggs, which are often located near the surface of the water,

especially those eggs spawned during the winter. Hunter et al. [48, 49] have noted an impact of UV-B radiation upon anchovy and mackerel eggs and yolk-sac larvae. Investigators have also described the impact of UV-B radiation upon marine copepods [50, 51], shrimp larvae, crab larvae, and euphausids [52, 53]. Results of the reports by Karansas et al. [48, 49] indicate that UV-B radiation increased mortality of the copepod populations and decreased fecundity of the survivors. Damkaer et al. [52, 53] have concluded that beyond threshold levels, activity, developmental rats, and survival rates of marine invertebrates are depressed by UV-B radiation. In a report of Jokiel [54], the author found that "shade-loving" sponges, bryozoans, and tunicates were killed by one to two days of exposure to solar UV radiation.

Field Validation of Laboratory Experiments

It is obvious from the references cited in the previous sections of this paper that UV-B radiation imposes a stress upon many living organisms. The question arises as to whether valid conclusions regarding the potential photochemical impact of stratospheric ozone depletion can be based on the laboratory experiments. For example, tests of more than 100 species or varieties of species in laboratory environmental growth chambers indicate that about 20% are sensitive to daily levels of UV-B exposure approximating levels currently found in Florida. Twenty percent were resistant to exposure levels four times greater than this, and the remaining 60% showed some intermediate sensitivity [55]. These tests would suggest that a significant fraction of the present agricultural varieties are currently under UV stress and would suffer decreased production with a 16% ozone reduction. However, tests of 15 species and varieties, irradiated in the field under conditions of high visible light and UV-A radiation, appeared to be more UV resistant than plants grown in the laboratory environmental growth chambers.

Where it is possible to make dose-response comparisons for various growth parameters for the same type of plants, the difference in resistance, comparing results from laboratory and field studies, is on the order of four-fold. If this result turns out to be general, the higher sensitivity indicated in the growth chambers does not represent what would happen in the field and the expected consequences of ozone depletion become considerably reduced. At this time, results from laboratory environmental growth chambers cannot be used to extrapolate to field conditions. However, they do provide a data base for identification of symptoms that might be encountered under stress from UV-B radiation [56].

There is evidence that some plant species acclimatize to enhanced levels of UV-B radiation. The occurrence of Temperate-Zone exotics at high elevations in the tropics, where the UV-B irradiance is significantly greater than that which would occur with a 16%

ozone reduction at temperate latitudes, attests to the ability of many species to acclimatize [57, 58]. If acclimatization to environments with high UV fluence is merely a phenotypic response, the rate at which atmospheric ozone depletion takes place would not matter. If, on the other hand, acclimatization involves genotypic changes for some species, the rate at which the atmospheric ozone layer changes must be considered. About half of the equilibrium ozone reduction is now predicted to occur within the next 30 years [55]. This may be insufficient time for genotypic changes to occur for long-lived plant species or for those that reproduce asexually.

Hunter et al. [59] evaluated the uncertainties in making an assessment of UV effects on natural anchovy populations. They concluded that a realistic assessment of the effects on the anchovy larval population requires knowledge of seasonal changes in larval abundance, incident UV-B radiation, spatial and temporal variation in the depth of penetration of UV-B radiation in the habitat, vertical distribution of larvae in the sea, rates of vertical mixing of eggs and larvae, and natural rates of mortality. At present, many of these parameters can only be approximated or are unknown for anchovy. Much less is known for most other species.

Hunter et al. [59] did not consider larval abundance a major uncertainty in their calculations for anchovy, but did consider it a major uncertainty in species where the seasonality of annual larval production is poorly defined. One of the principal reasons that they considered the relative effect of increased UV radiation due to an ozone decrease to be minor is that anchovy larvae are abundant at other depths as well as in the upper few meters. A 25% reduction in ozone in moderately productive waters is equivalent to about a one-meter increase in the depth of penetration of the biologically effective UV-B radiation for anchovy larvae. An increase in depth of penetration of one meter would not have a major effect on a population distributed over about 60 meters. Calkins and Thordardottir [37] have pointed out that reproduction by surviving organisms could replace those killed by UV-B radiation. As long as the dose of UV-B radiation does not exceed a certain "replacement limiting dose" for each species of organism then, according to the model, populations could survive.

Large uncertainties for the impact of UV-B radiation upon anchovy larvae are associated with vertial distribution and mixing, and it is unrealistic to establish upper and lower limits for these variables. The number of larvae present in tows taken at a 2-m depth can vary from 0.25% to 27% of the population and may be dependent on the depth of the mixed layer [59]. Thus, seasonal changes in vertical distribution, or possible biases in calculating the average distribution, could either increase, or reduce to nearly zero, estimated UV effects. Similarly, vertical mixing could reduce estimated UV effects to zero at current or reduced ozone concentrations.

Hunter et al. [59] concluded that the parameters of vertical distribution and mixing could account for the full range of possible UV-B effects on the population independent of all other variables.

Simulation of Solar UV-B Radiation

Experimental enhancement of UV-B radiation for ozone depletion studies occurs through use of artificial sources - sources whose spectral output cannot conform exactly to the solar spectrum. Due to this lack of conformity and because not all wavelengths of UV radiation are equally effective in producing biological effects, the relative biological effectiveness of radiation in the UV waveband must be determined in order to compare the results of the experiments with what might occur in nature. Photobiological action spectra demonstrate the relationship between biological effectiveness and wavelength of incident radiation. Analytic representations of action spectra can then be used to weight the spectral irradiance of interest. Weighting the irradiance over all wavelengths yields the biologically effective irradiance.

This approach presupposes knowledge of the action spectrum of interest. Usually the selection of a weighting function occurs "after the fact" by determining which of the published action spectra best "fits" the data in question, not an unrealistic approach if there are no other practical alternatives. For example, Smith and Baker [60, 61] and Smith et al. [34] have demonstrated that results of acute radiocarbon uptake studies with marine algae are consistent with a photoinhibition action spectrum [62], but results of chronic exposures [33] appear to be best described by an analytic representation [63] of a DNA action spectrum [64]. The results of a study by Worrest et al. [35] were evaluated utilizing the absolute dose as well as three different biologically effective doses: one weighted by a generalized plant action spectrum [65], another by a DNA action spectrum [64], and the third by a photoinhibition action spectrum [62]. There was a trend favoring the biologically sensitivity functions weighted more heavily at the shorter wavelengths (plant and DNA) rather than the photoinhibition action spectrum which has a "flatter" response or a response more closely resembling the absolute irradiance spectrum.

The major uncertainty associated with the calculation of the biologically effective irradiance is introduced by the choice of weighting function. As an example, in the report by Worrest et al. [35], a level of irradiance selected in an experiment performed during the fall of the year was determined by weighting the irradiance from the artificial UV-B source by a generalized plant action spectrum [65]. Two of the treatments were designed to simulate a current level of plant-effective irradiance for October and a plant-effective irradiance simulating a 15% ozone reduction [66]. The components of the marine ecosystem under study were naturally re-

cruited from existing populations in Yaquina Bay (Oregon). If the sensitivity of responses for the components of the experimental ecosystems was consistent with a generalized plant action spectrum, the lack of conformity between the artificial UV-B sources and the existing solar radiation would be inconsequential. However, if the impact of the UV-B waveband upon the ecosystem was more consistent, for example, with a DNA action spectrum [64], the experimental design would have been simulating the solar conditions in August rather than October, and a 19% ozone reduction rather than a 15% ozone reduction.

An additional complication in experimental studies is that, in most situations, the artificial UV-B sources are turned on at a single irradiance level for from 4-6 hours to obtain a given daily dose comparable to that from the sun. This is obviously unnatural and subjects organisms to much higher exposures thatn the sun at some times and possibly lower doses than from the sun at noon.

Traditionally, biological action spectra have been determined by exposing organisms to monochromatic radiation at the same irradiance and scoring the biological response, or by supplying the level of monochromatic fluence necessary to elicit a certain biological endpoint. In either case, the emphasis has been to determine the fine structure of the action spectrum with as much spectral resolution as possible in order that potential chromophores might be identified. Seldom have the tails of these action spectra been elucidated, because usually they contribute little to identification of chromophores. Since solar spectral irradiance changes by orders of magnitude within the UV spectrum, tails of action spectra can be quite important even though these may represent greatly diminished biological effectiveness compared to the maxima. Thus, the spectra to be used as weighting functions should ideally include any tails that lie within the waveband where there is solar flux.

Since biological action spectra are normally determined with monochromatic radiation, the assumption must be made that radiation at different wavelengths does not interact when presented simultaneously. There is evidence that synergisms may be involved when organisms are exposed to polychromatic UV radiation. For example, there was a close correspondence between the action spectrum for a particular type of DNA lesion, pyrimidine dimers, and death of cultured Chinese Hamster cells over a broad waveband from 254 to 313 nm when the action spectrum was determined with monochromatic radiation [67]. However, in a comparison of responses of the same type of cell cultures to monochromatic 254 nm radiation and polychromatic UV-B from a sunlamp, the survival curves and DNA lesion frequencies did not support the hypothesis that the same DNA photolesion was primarily responsible for cell death [68, 69]. Thus, polychromatic UV-B radiation may produce different kinds and proportions of DNA photolesions than monochromatic UV radiation. These differences in

turn may result in different physiological responses. For cultured mammalian cells, this was expressed in different characteristic survivorship curves.

Such evidence should encourage caution in the application of action spectra determined with monochromatic radiation. Various repair systems activated by light may also complicate spectral assessments. Photoreactivation is a process that repairs a certain type of DNA damage. This mechanism is driven by long-wavelength UV and short-wavelength visibile radiation and can greatly diminish the resultant damage caused by UV-B radiation. Plant photosynthesis also appears to be much less inhibited by UV-B radiation in the presence of strong visibile radiation than if leaves are subjected only to UV-B radiation or to UV-B radiation in conjunction with dim visible radiation. Although it is unlikely that photoreactivation per se is effective in repairing photosynthetic damage, some mechanism is operating to alleviate the inhibition. Thus, repair systems or other interactions that might alter the expression of UV damage in plants diminishes the usefulness of biological action spectra determined with monochromatic radiation. To be useful in an ecological context, weighting functions should be verified by exposing organisms to different spectral distributions of polychromatic radiation to determine if the response is consistent with a proposed action spectrum. Such an approach has seldom been undertaken.

Epilog

Although an assessment of the impact of enhanced levels of UV-B radiation upon the biosphere is fraught with complications and caveats, the evidence that solar UV-B radiation is a stressful agent is growing. It has been demonstrated that exclusion of solar UV-B radiation from the current solar spectrum enhances primary production [28, 29, 70]. Although it does not necessarily follow that enhanced levels of solar UV-B radiation will further decrease productivity from current levels, one might assume that organisms do not possess repair mechanisms which function to "pre-adapt" the organism to levels of radiation not previously encountered [71].

As determined from the work of Van Dyke and Thomson [30], alteration of a marine algal community structure may result from exposure of microcosms to enhanced levels of UV-B radiation. A similar impact of UV-B radiation on the community structure of marine microcosms was noted by Worrest et al. [31]. Also noted in the latter study was depressed chlorophyll a concentrations, reduced biomass, and increased autotrophic indexes. Both of these studies utilized artificial (relatively low-level) light sources in the laboratory, whereas in an investigation by Worrest et al. [35], marine microcosms were exposed to about 90% of the natural, visible fluence. The results of the study parallel those found by Worrest et al. [31] and Van Dyke and Thomson [30] which, in part, corrobrates the previous laboratory results.

There are, also, subtle effects of solar UV-B radiation mentioned in the literature which may have a significant impact upon ecosystems. In some cases plant growth [17] and shellfish and finfish reproduction [53, 59] are restricted to certain times of the year, usually spring. The environmental factors influencing this period of development involve temperature, moisture, day length, nutrients, and possibly other factors. The amount of UV-B radiation early in the growing season, when young UV-B-radiation-sensitibe plants and animals are developing, may not exceed the threshold under unperturbed conditions. However, given a reduction of stratospheric ozone, the UV-B irradiance may exceed threshold levels for some days, thus shortening the reproduction/development period.

Karanas et al. [51] have noted that the fecundity of a marine copepod is reduced by nonlethal levels of UV-B radiation. This impact upon reproductive rates was also noted by Worrest et al. [36] and utilized to determine the impact of enchanced UV-B radiation upon a model ecosystem. Shifts in community composition occurred in the model, a result corroborated by a subsequent study involving naturally recruited marine ecosystems [35]. Fox and Caldwell [72] noted a similar shift resulting from UV-B exposure in an investigation into the competitive interaction between pairs of plant populations.

The interpretations of changes in community diversity is subject to speculation; but one can say that, if the species composition of the primary producers is altered, the quality and possibly the quantity of food present for primary consumption could also be altered. Therefore, organic carbon exchange between trophic levels could be affected. The impact would be significant if the organisms selected for by enhanced UV-B radiation were of lower nutritional value (i.e., if they impacted growth and fecundity of the consumers). Another effect might be to alter the size distribution of the component producers in the ecosystem. For example, in a marine ecosystem, decreasing the size of the representative producers upon which consumers graze can significantly increase the energy allotment required for consumption, thereby reducing the feeding efficiency of the consumer. As stated by Worrest et al. [35], the actual impact of altering the community composition of an ecosystem requires further investigation.

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